Lower and Upper Devonian brachiopods from the Budleigh Salterton Pebble Bed, Devon.

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SYNOPSIS. Since the mid nineteenth century, Devonian brachiopods have been identified from constituent pebbles in the Triassic at Budleigh Salterton. However, only now can they be recognized as coming from quartzite pebbles of two separate Devonian ages: (a) Lochkovian – Pragian, corresponding in facies and fauna to the Landévennec and Gahard Formations of France (previously termed the Grès à *Orthis monnieri*) and (b) Frasnian, with a fauna not corresponding directly with that from any other European quartzite. The brachiopod species originally described by Salter and Davidson are refigured and allotted to more modern genera, and fresh plate descriptions are presented to Davidson's 1881 Monograph on the Budleigh Salterton brachiopod fauna, including both Ordovician and Devonian species. The new species *Salopina adventita* is described, of lower Devonian age. Lectotypes are selected of the following nominal species of Davidson: *Crania transversa, Nucleospira vicaryi, Orthis vicaryi, Rhynchonella valpyana, R. vicaryi, R.? ovalis, Spirifera macroptera var. microptera, Strophomena edgelliana, S. etheridgii, S. rouaulti*; and of Salter Spirifer antiquissimus and Leptaena vicaryi.

INTRODUCTION

Since 1835, Palaeozoic faunas have been known in the Budleigh Salterton Pebble Bed of Triassic age, which outcrops along the cliffs for 2 km at Budleigh Salterton, Devon, and from which pebbles are found on the adjacent beach. The brachiopods were first described by Salter (1864), who recognized their central European affinities, but who failed to realise that more than a single geological age was represented. The fauna was subsequently described in more detail by T. Davidson in a series of publications (1866-71, 1870, 1880, 1881), who realised that three separate ages were involved; in modern terms Arenig, Llandeilo and Devonian. The Arenig and Llandeilo forms have been revised by Cocks & Lockley (1981). However, Davidson, although he correctly attributed some of the Devonian forms to French species, did not realise that at least two different Devonian ages were involved. Some of the brachiopod species can be attributed to the Lower Devonian, and can still be directly compared with some forms from France, for example the Landévennec and

Gahard Formations (formerly known as the Grès à Orthis monnieri) of late Gedinnian or early Siegenian (Lochkovian-Pragian) age. The remainder of the fauna (including the spiriferides which Salter thought to be the oldest in the geological record) can be attributed to the Upper Devonian, specifically the Frasnian, although there are no quartzites of that age known from France, Belgium or Germany which carry the same fauna as that from Budleigh Salterton.

The British Museum (Natural History) is fortunate in possessing the most comprehensive collections of the Budleigh Salterton faunas, which were built up by two amateurs, W. Vicary and R.H. Valpy and bequeathed to the Museum in 1903 and 1905 respectively, and from which the bulk of Salter's and Davidson's species were described. The opportunity is taken here not only to refigure the Devonian forms and assign the older names to more modern genera, but also to present revised plate descriptions to Davidson's Palaeontographical Society Monograph of the Budleigh Salterton brachiopods (1881) in a similar way to those plate descriptions already presented for the Lower Palaeozoic of Britain (Cocks 1978).

AGE OF THE FAUNAS

The brachiopods which occur in the Budleigh Salterton pebbles can now be attributed to four different ages.

Ordovician

These faunas are described in Cocks & Lockley (1981), although revised plate descriptions to Davidson's monograph (1881) are presented in the Appendix here (p. 34). The brachiopods identified from the Middle Arenig are *Lingulobolus hawkei* (Rouault, 1850), *Lingulobolus brimonti* (Rouault, 1850), *Pseudobolus? salteri* (Davidson, 1866), *Ectenoglossa lesueuri* (Rouault, 1850) and possibly *Philhedrella? vicaryi* (Davidson, 1866), and from the late Llandeilo *Tafilaltia valpyana* (Davidson, 1869), *Salopia? pulvinata* (Salter, 1864), *Corineorthis erratica* (Davidson, 1869) and *Porambonites* sp. In addition, the species identified and illustrated by Davidson as '*Lingula' morieri* Tromelin, 1876 is almost certainly an Ordovician rather than a Devonian form.

Devonian

Davidson considered that all the Devonian faunas belonged to the Lower Devonian, although he was puzzled (1882:356) by the downward extension of the range of certain spiriferides. Now that more is known about Devonian brachiopods, it is clear that some of the Budleigh Salterton species are Lower Devonian, in particular from beds which must lie close to the Gedinnian-Siegenian boundary, including such well-known forms as Platyorthis monnieri, and that others, such as Cyrtospirifer verneuili, are of Upper Devonian, Frasnian, age. A close analysis of all the available pebbles confirms, not only that brachiopods of these two different ages do not co-occur on a single pebble, but also that virtually all of the varied Devonian fauna can be firmly attributed to one or other of these two ages. Some of the co-occurrences are documented in the systematic section below. The full list is as follows.

From the Gedinnian-Siegenian (Lockhovian-Pragian) pebbles came Platyorthis monnieri (Rouault, 1851), Salopina adventita sp. nov. (p. 24), Leptostrophia etheridgii (Davidson, 1870), Shaleria vicaryi (Davidson, 1870), Mclearnites rouaulti (Davidson, 1870), Schuchertella? sp., Katunia? vicaryi (Davidson, 1870), 'Camarotoechia' ovalis (Davidson, 1870), Nucleospira vicaryi Davidson, 1870, Athyris? incerta Davidson, 1870, Howellella cortazari Carls, 1969 and Mutationella? erratica (Davidson, 1870), and possibly Cryptonella? cf. rhenana (Drevermann, 1902). From the Frasnian pebbles came Petrocrania transversa (Davidson, 1870), Rhipidomella? budleighensis (Davidson, 1870), Douvillina edgelliana (Davidson, 1870), Douvillina? budleighensis (Davidson, 1870), Anoplia sp., Productella vicaryi (Salter, 1864), uncinuliform sp. indet., 'Camarotoechia' valpyana (Davidson, 1870), Cyrtospirifer verneuili (Murchison, 1840), Cyrtospirifer? micropterus (Davidson, 1870) and Cryptonella? sp.

In addition, there are various nominal species, 'Orthis hamoni Rouault' of Davidson, 'Rhynchonella' winwoodiana Davidson, 1870, 'Rhynchonella elliptica Schnur' of Davidson and 'Rhynchonella thebaulti Rouault' of Davidson, all of Devonian age and which remain unidentifiable for various reasons discussed below, and a small inarticulate, Philhedrella? incerta (Davidson, 1870), which could be of either Ordovician or Devonian age.

SYSTEMATIC PALAEONTOLOGY

All the species described from the Devonian pebbles in the Budleigh Salterton conglomerate are reviewed in turn below, and some hitherto undescribed forms, *Salopina adventita* sp. nov., *Schuchertella*? sp., *Anoplia* sp., and some terebratulides, are also illustrated for the first time. Those species described by Davidson and Salter are all ascribed to modern genera, apart from 'Orthis hamoni', discussed under the Enteletacea and the Rhynchonellida below.

The specimen repositories are as follows: British Museum (Natural History), B, BB and BC; Sedgwick Museum, Cambridge, SM; British Geological Survey, GSM; Bristol City Museum, BRSMG; the Albert Memorial Museum, Exeter, Ex M; Royal Geological Society of Cornwall, RGSC; and the Royal Museum of Scotland, Edinburgh, RSM.

> Class INARTICULATA Order ACROTRETIDA Kuhn Suborder CRANIIDINA Waagen Superfamily CRANIACEA Menke Family CRANIIDAE Menke

Genus PETROCRANIA Raymond, 1911

Petrocrania transversa (Davidson, 1870)

Fig. 1

- 1870 Crania transversa Davidson: 78; pl. 4, figs 9, 10.
- 1881 Crania transversa Davidson; Davidson: 352; pl. 40, figs 9, 10.

LECTOTYPE (here selected) B 21544, the original of Davidson 1870: pl. 4, fig. 9 (and also of Davidson 1881: pl. 40, fig. 10).

DISCUSSION. The original specimen occurs on a slab with the common late Devonian rhynchonellide termed by Davidson *Rhynchonella inaurita* and so there is no doubt as to its age. Only a single valve is now in the Vicary Collection, although Davidson's original description speaks of two. The generic attribution is due to the fact that the anterior adductor scars are relatively smaller than the posterior scars and the apparent absence of ornament (although only the internal mould of the valve is known and so the possibility of a fine ornament cannot be entirely ruled out).

Class ARTICULATA Order ORTHIDA Schuchert & Cooper Suborder ORTHIDINA Schuchert & Cooper Superfamily ENTELETACEA Waagen

The Budleigh Salterton enteletaceans of Devonian age consist of the three species described below, two from the Lower Devonian and one from the Upper Devonian. Not revised is the species described by Davidson (1881: 344, fig. 20) as *Orthis hamoni* Rouault. Rouault's original material from the Lower Devonian of Gahard, France has not been traced in the University of Rennes. Those specimens illustrated by Davidson are the only two known from Budleigh Salterton



Fig. 1 Petrocrania transversa (Davidson, 1870). Lectotype (here selected), B 21544, internal mould, × 2.

- Figs 2-6 Platyorthis monnieri (Rouault, 1851). Fig. 2, B 21586, internal moulds of pedicle valves, × 1.5; Fig. 3, B 13283, internal mould of brachial valve, × 2; Fig. 4, BC 6573, internal mould of pedicle valve, × 2; Fig. 5, BC 6574, internal mould of brachial valve, × 2; Fig. 6, BB 70329, internal mould of pedicle valve, figured Davidson 1881: pl. 40, fig. 6, × 2.
- Figs 7-9 Salopina adventita sp. nov. Fig. 7, BC 6577, internal mould of brachial valve, × 3; Fig. 8a, b, holotype BC 6576, latex cast and internal mould of pedicle valve, × 3; Fig. 9, BC 6575, internal moulds of a pedicle valve and several brachial valves, and a brachial valve of Katunia? vicaryi, × 4.
- Fig. 10 Rhipidomella? budleighensis (Davidson, 1870). Holotype B 21412, internal mould of pedicle valve, the original of Davidson 1870: pl. 4, fig. 14, × 1.5.

(Davidson 1881: 345) and they are both on a single block. This block, which also includes the type of *Rhynchonella winwoodiana* Davidson, was in the Winwood collection, but it has not been traced in that collection in the Bristol City Museum. All that can be determined from Davidson's drawings is that the form is an enteletacean.

Family DRABOVIIDAE Havlíček

Genus SALOPINA Boucot, 1960

Salopina adventita sp. nov.

Figs 7–9

DIAGNOSIS. *Salopina* with planoconvex brachial valve, subcircular outline, weak dorsal sulcus, fine costellae, and divergent brachiopores of medium length.

NAME. 'Coming from abroad.'

DESCRIPTION. *Exterior*. Pedicle valve convex, brachial valve planoconvex with weak dorsal sulcus and corresponding ventral fold; outline subcircular with relatively narrow hinge line. Small open delthyrium, and small curved apsacline pedicle interarea under uncurved umbo; brachial valve interarea very small, with umbo scarcely developed. Ornament of relatively fine costellae with characteristic salopinid branching and midline (Walmsley 1965: fig. 1). Occasional poorly developed growth lines seen.

Pedicle valve interior. Strong pair of teeth, supported by dental lamellae which merge with the floor posteriorly to the anterior end of the teeth. Relatively poorly developed impressions of the muscle field, which is unenclosed anteriorly. No trace of mantle canals and the valve interior is smooth except at the periphery where reflections of the external costellae may be seen.

Brachial valve interior. Small, linear to slightly pear-shaped cardinal process. Strong brachiophores which also act as the anterior part of the socket, the brachiophores of medium length for the genus and which are quadrilateral to spearshaped at their bases and which extend anteriorly into raised muscle-bounding ridges in adult specimens (e.g. Fig. 9, lower left), which may extend for over half the valve length. The brachiophores diverge at angles from 65° to 90°. Central myophragm variably impressed, sometimes nearly strong enough to be called a weak septum. Adductor muscle field variably impressed, not usually separated posteriorly and anteriorly, and seldom with any trace of an anterior margin.

MATERIAL. Holotype BC 6576 (Fig. 8), the internal mould of a pedicle valve. Additional material: 12 other pedicle valves and 5 brachial valves on the same block as the holotype, including BC 6575 (Fig. 9), BC 6577 (Fig. 7); 2 pedicle valves and 7 brachial valves on the block registered B 21539, BC 6087–8 (including one broken brachial valve illustrated under *Leptostrophia etheridgii* in Fig. 19); and smaller numbers of both valves on other blocks.

DIMENSIONS (in mm)

	Length	Width
pedicle valve, holotype	6.1	6.6
pedicle valve	6.5	6.2
pedicle valve	5.8	5.5
brachial valve	5-5	7.4
	pedicle valve, holotype pedicle valve pedicle valve brachial valve	Lengthpedicle valve, holotype6·1pedicle valve6·5pedicle valve5·8brachial valve5·5

DISCUSSION. Walmsley et al. (1969) have given a useful review of the ten species which had been described up to that time and which they ascribe to Salopina. Since then, other Silurian and later species have included Salopina sp. and S. kosoviensis described by Havlíček (1977) from the Motol Formation (Wenlock) and Kopanina formation (Ludlow) respectively of Bohemia; S. brandi described by Cocks (1979) from the Qarabil Formation (Wenlock) of Iran, S. walmsleyi described by Isaacson (1977) from the Lower Devonian of Bolivia; S. boucoti described by Sheehan (1976) from the Upper Silurian of Utah; S. onukii, S. o. elongata and S. yamadai described by Tachibana (1976, 1980) from the Silurian of Japan; S. delta and S. submurifer described by Johnson, Boucot & Murphy (1973, 1976) from the Upper Silurian and Lower Devonian of the Roberts Mountains, Nevada, U.S.A.; S. kemezysi Chatterton (1973) from the Lower Devonian of New South Wales; S.? yichangensis Rong & Yang (1981) from the Silurian of China; S. kokbaitalensis Ushatinskaya & Nilova (1975) from the Lower Devonian of Kazakhstan, U.S.S.R.; S. aspera Xu (1979) from the Tangxiang Formation (L. Devonian), Guangxi, China, and S. mediocostata Strusz (1982) from the Upper Silurian of Canberra, Australia. Thus Salopina now includes some 27 nominal species, although a complete review of the genus is outside the scope of the present work. Nevertheless, by the specific criteria nominated by Walmsley et al. (1969: table 2), S. adventita still differs from the other species by the combination of characters mentioned in the diagnosis.

Family RHIPIDOMELLIDAE Schuchert Subfamily RHIPIDOMELLINAE Schuchert

Genus RHIPIDOMELLA Oehlert, 1890

Rhipidomella? budleighensis (Davidson, 1870) Fig. 10

1870 Athyris? budleighensis Davidson: 80; pl. 4, fig. 14.
1881 Athyris budleighensis Davidson; Davidson: 338; pl. 38, fig. 6.

HOLOTYPE (by monotypy). ... The internal cast of a ventral valve has alone been discovered ... found by Mr Vicary along with *Spirifera Verneuilii* and *Rhynchonella inaurita*' (Davidson 1870: 80); B 21512, the original of Davidson 1870: pl. 4, fig. 14.

DISCUSSION. The holotype is poor, although it is certainly an enteletacean and not an athyrid, as thought by Davidson. It is a rhipidomellid; it may or may not be a *Rhipidomella, sensu stricto*, since the peripheral crenulations characteristic of the genus are not visible in the poor preservation. It is associated with an upper Devonian *Cyrtospirifer* and large rhynchonellide, and so its age is not in doubt – the only other rhipidomellids of middle and upper Devonian age (Boucot *et al.* 1965) are *Thiemella* and *Aulacella*, both of which have distinctive shell shapes. In addition to the holotype, there is another specimen in the Vicary Collection, B 21713, in which the muscle field can be seen more clearly.

Subfamily PLATYORTHINAE Harper, Boucot & Walmsley Genus PLATYORTHIS Schuchert & Cooper, 1931

Platyorthis monnieri (Rouault, 1851)

Figs 2-6

- 1851 Orthis Monnieri Rouault: 376.
- 1870 Orthis Vicaryi Davidson: 84; pl. 5, figs 20-22.
- 1881 Orthis Monnieri Rouault; Davidson: 345; pl. 4, figs 1-8.
- 1972 Platyorthis monnieri (Rouault) Renouf: 108; pl. 22, figs 7–15; pl. 23, figs 1–7.

TYPE SPECIMENS. Renouf (1972: 109) states that the types of *monnieri* have not yet been found in Rouault's collection at the University of Rennes. Lectotype of *vicaryi* (here selected) B 20940, the original of Davidson 1870: pl. 5, figs 20 (right-hand side), 21 and 22.

DISCUSSION. This distinctive species is by far the most common Lower Devonian brachiopod in the Budleigh Salterton Pebble Bed, and several hundred specimens have been obtained by a variety of collectors. The species has been extensively revised by Renouf (1972), and indeed he used some Budleigh Salterton material in his redescription of the Brittany material from the eponymous Grès à Orthis monnieri of Gedinnian or Siegenian age.

Order STROPHOMENIDA Öpik Suborder STROPHOMENIDINA Öpik Superfamily STROPHOMENACEA King Family STROPHEODONTIDAE Caster Subfamily DOUVILLININAE Caster

Genus DOUVILLINA Oehlert, 1887

Douvillina edgelliana (Davidson, 1870)

1870 Strophomena Edgelliana Davidson: 86; pl. 6, figs 2-5.

Figs 21-22

- 1881 Strophomena Edgelliana Davidson; Davidson: 349; pl. 39, figs 5-7.
- 1978 Douvillina edgelliana (Davidson) Harper & Boucot: 151.

LECTOTYPE (here selected) B 21534, internal mould of a brachial valve, the original of Davidson 1870: pl. 6, figs 3, 4 and Davidson 1881: pl. 39, figs 7, 7a, and its counterpart, external mould of a brachial valve, the original of Davidson 1870: pl. 6, fig. 2 and Davidson 1881: pl. 39, fig. 6, refigured here as Fig. 21.

DISCUSSION. Three matching pieces survive of the pebble containing the lectotype and these contain the internal mould of a pedicle valve (Fig. 22), poorly preserved external and internal counterparts of another pedicle valve and external and internal counterparts of two brachial valves, one of which is the lectotype (Fig. 21). These stropheodontids are associated on the same pebble with numerous specimens of Anoplia sp., discussed below, and are, like all the species of Douvillina, sensu stricto, discussed by Harper & Boucot (1978: 150-1) of late Devonian (Frasnian) age. The species has a pedicle valve of medium to weak convexity and a brachial valve which is almost flat, excluding it from the resupinate Douvillinoides and the biconvex Douvillinaria. Although the type species of Douvillina, D. dutertrii (Murchison), has not been revised, the distinctive brachial valve structures of edgelliana are very close to the form illustrated by Harper & Boucot (1978: pl. 26, figs 17a, b) as Douvillina cf. dutertrii from the late Frasnian of the Spanish Sahara.

Douvillina? budleighensis (Davidson, 1870) Fig. 13

- 1870 Strophomena budleighensis Davidson: 86; pl. 6, fig. 1. 1881 Strophomena Budleighensis Davidson; Davidson:
- 349; pl. 39, figs 4, 4a, b.
- 1978 Douvillina budleighensis (Davidson) Harper & Boucot: 151.

HOLOTYPE (by monotypy). 'Of this species a remarkable internal cast of the ventral valve only has been found' (Davidson 1870: 86), B 21538, the original of Davidson 1870: pl. 6, fig. 1 and Davidson 1881: pl. 39, figs 4, 4a, b; refigured here as Fig. 13.

DISCUSSION. The holotype is still the only known specimen and consists of the internal mould of a pedicle valve. There is no counterpart, and so the nature of the ornament is unknown, which would be of systematic importance. The specimen is comparable with that illustrated as Douvillina cf. cayuta (Hall) by Harper & Boucot (1978: pl. 26, fig. 11) from the Chemung Group of Frasnian age in New York State, and so Davidson's species is assigned to Douvillina with a query. There are no other identifiable specimens on the type pebble, but the species is assigned here to the upper Devonian part of the Budleigh Salterton fauna on the basis of comparison with the New York form. Douvillina, senso stricto, has a range restricted to the Frasnian (Harper & Boucot 1978: 20). D.? budleighensis is much more convex and has a relatively larger muscle field than Douvillina edgelliana from Budleigh Salterton, and it seems most unlikely that they are conspecific.

Genus MCLEARNITES Caster, 1945

Mclearnites rouaulti (Davidson, 1870) Figs 11–12

- 1870 Strophomena Rouaulti Davidson: 85; pl. 6, figs 8, 9.
 - 1881 Strophomena sp. Davidson: pl. 39, figs 1a, b.
- 1881 Strophomena Rouaulti Davidson; Davidson: 348; pl. 39, fig. 9.
- 1972 Douvillina (Mesodouvillina) lecaroensis Renouf: 111; pl. 23, figs 8–16; pl. 24, figs 1, 7, 9.
- 1978 Mclearnites (Mclearnitesella) lecaroensis (Renouf) Harper & Boucot: 132.

LECTOTYPE of *rouaulti* (here selected), B 21540, internal mould of a brachial valve, figured Davidson 1870: pl. 6, fig. 8 (left) and also Davidson 1881: pl. 39, fig. 9c, refigured here as Fig. 12. There is also the internal mould of a pedicle valve on the same slab.

DISCUSSION. Only three pedicle valves and one brachial valve are known of this species from Budleigh Salterton; nevertheless it is distinctive and clearly attributable to *Mclearnites*. It is also the same form as that named *Douvillina (Mesodouvillina) lecaroensis* by Renouf (1972) from the Grès à *Orthis monnieri* of Brittany, which has already been attributed to *Mclearnites* by Harper & Boucot (1978: 132). The latter distinguish two subgenera based on minor ribbing differences and a third based on what they term a geniculation, but in my opinion the genus need not be subdivided above the species level.





Fig. 13 Douvillina? budleighensis (Davidson, 1870). Holotype B 21538, internal mould of pedicle valve, figured Davidson 1870: pl. 6, fig. 1, × 2.

- Figs 14-17 Shaleria vicaryi (Davidson, 1870). Fig. 14a, b, BC 6088, latex cast and internal mould of pedicle valve, × 2; Fig. 15, B 21637, internal mould of brachial valve, × 2; Fig. 16, B 21638, internal mould of brachial valve, × 2; Fig. 17, holotype B 21537, internal mould of pedicle valve, figured Davidson 1870: pl. 6, figs 6, 7, × 2.
- Figs 18-20 Leptostrophia etheridgii (Davidson, 1870). Fig. 18, BC 6579, internal mould of brachial valve, × 1.5; Fig. 19, BC 6088, internal mould of pedicle valve, × 2; Fig. 20, lectotype (here selected), B 21539, latex cast of an internal mould of a brachial valve, figured Davidson 1870: pl. 6, figs 10 and 11, × 1.8.
- Figs 21, 22 Douvillina edgelliana (Davidson, 1876). Fig. 21a, b, lectotype (here selected), B 21534, latex cast and internal mould of a brachial valve, figured Davidson 1870: pl. 6, figs 3 and 4, × 2. Fig. 22, B 21541, internal mould of pedicle valve, figure Davidson 1870: pl. 6, figs. 5, × 1.5.

Genus SHALERIA Caster, 1939

Shaleria vicaryi (Davidson, 1870)

Figs 14-17

1870 Strophomena Vicaryi Davidson: 86; pl. 6, figs 6, 7.
1881 Strophomena Vicaryi Davidson; Davidson: 348; pl. 39, fig. 8.

HOLOTYPE (by monotypy). '... We are at present acquainted with one valve only' (Davidson 1870: 86); B 21537, the internal mould of a pedicle valve, the original of Davidson 1870: pl. 6, figs 6, 7, and Davidson 1881: pl. 39, fig. 8, refigured here as Fig. 17.

DISCUSSION. The holotype occurs on a piece of pebble without other fauna apart from the external impression of a flat strophomenide valve which may or may not be the same species. There are four other large pieces of pebble containing stropheodontids which are grouped here as being conspecific with the holotype, even though none of the pedicle valves on these slabs (e.g. Fig. 14) are quite as convex as the holotype (Fig. 17). The species is associated on the slabs with Leptostrophia etheridgii and Salopina adventita and is thus undoubtedly of lower Devonian age. The generic attribution is fairly certain, but the subgenus is less clear-cut - the three described by Harper & Boucot (1978: 161-4), S. (Shaleria), S. (Janiomya) and S. (Protoshaleria), all differ in some ways from S. vicaryi and thus no subgenus will at the moment be specified for the Budleigh Salterton form. None of the specimens has a definite counterpart, but from isolated impressions of shell fragments on the same pebbles, it seems probable that S. vicaryi lacks the interrupted ornament so widespread amongst species of Shaleria, for example the wellknown S. ornatella from the late Silurian of the Welsh Borderland.

Subfamily LEPTOSTROPHIINAE Caster

Genus LEPTOSTROPHIA Hall & Clarke, 1892

Leptostrophia etheridgii (Davidson, 1870) Figs 18-20

- 1870 Strophomena Etheridgii Davidson: 85; pl. 6, figs 10-12.
- 1881 Strophomena? sp. Davidson: 350; pl. 39, fig. 2, non fig. 1.
- 1881 Strophomena Etheridgii Davidson; Davidson: 350; pl. 39, figs 10, 11.

LECTOTYPE (here selected), B 21539, internal mould of a large brachial valve, the original of Davidson 1870: pl. 6, figs 10, 11 and Davidson 1881: pl. 39, fig. 10 (refigured here as Fig. 20).

DISCUSSION. The species includes the largest strophomenide valves found at Budleigh Salterton (Fig. 20). One brachial valve interior and 8 pedicle valve interiors are present on the lectotype pebble, as well as specimens of *Shaleria vicaryi*, *Salopina adventita* and '*Camarotoechia*' ovalis; one pedicle valve interior, two brachial valve interiors (incl. Fig. 18) and many exteriors of both valves are preserved on another pebble, BC 6579, with the same associated fauna. The species is thus clearly of Lower Devonian age. The parvicostellae are of more or less equal size and thus the species can be attributed to *Leptostrophia* rather than *Mesoleptostrophia*, using the criteria of Harper & Boucot (1978), although I do not agree with those authors that these relatively minor ornamental changes should command subfamilial recognition in taxonomy.

Superfamily DAVIDSONIACEA King Family SCHUCHERTELLIDAE Williams

Genus SCHUCHERTELLA Girty, 1904

Schuchertella? sp.

Figs 23-24

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?1870 Streptorhynchus crenistria Phillips; Davidson: 87; pl. 5, fig. 26.
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- ?1881 Orthis hipparionyx? Vanuxem; Davidson: 347; pl. 39, non figs 1a, 1b.
- ?1881 Streptorhynchus crenistria? Phillips; Davidson: 351; pl. 39, fig. 3.

The original of Davidson's figures of 'Streptorhynchus crenistria' (1870: pl. 5, fig. 26 and 1881: pl. 39, fig. 3), B 20901, is merely a fragment of probable davidsoniacean shell. Whether or not this is conspecific with the other specimens figured here must remain for ever doubtful: it is certainly much larger. The original of Davidson's 'Orthis hipparionyx' is an internal mould of a broken pedicle valve associated with a specimen of Mclearnites rouaulti and so is of early Devonian age: but it is doubtful whether that valve is of the same species as those illustrated here (Figs 23-24). Nevertheless, the brachial valve (Fig. 24) is associated on the same pebble with Howellella cortazari and is thus also of early Devonian age. It is undoubtedly a davidsoniacean, and very probably of the same species (it has the same ribbing style and general proportions) as the pedicle valve on another pebble (Fig. 23). The generic identification is more difficult, since early Devonian davidsoniaceans wait to be comprehensively reviewed, and thus the form is identified merely as Schuchertella? sp. for the present.

Suborder CHONETIDINA Muir-Wood Superfamily CHONETACEA Bronn Family ANOPLIIDAE Muir-Wood

Genus ANOPLIA Hall & Clarke, 1892

Anoplia sp.

Figs 25-28

- 1870 Chonetes sp. Davidson: 87; pl. 6, fig. 13.
 1881 Chonetes sp.? Davidson; 352; pl. 39, figs 12, 13.
- 601 Choneles sp.: Davidson, 552, pl. 57, ligs 12, 15.

It is unfortunate that the rock in which the specimens of Anoplia have been found is a relatively coarse quartzite, so that the finer details of morphology and possible ornamentation are not preserved, otherwise this chonetid would warrant formal description and the creation of a new specific name. There are quite a number of specimens available; eight pedicle valve internal moulds and three brachial valve internal moulds, plus several external moulds on one pebble (including BC 6580-83, Figs 25, 26, 28); twelve pedicle valves and three brachial valves on another (including B 14198, Fig. 27); four pedicle valves and two brachial valves on a third pebble, which also carries the type specimens of Douvillina edgelliana of undoubted Frasnian age; and also some other material. The species also co-occurs on pebbles with the large indeterminate uncinuliform (p. 31). This extends the age range of Anoplia upwards from the Emsian (Boucot & Harper 1968),



29a



30

- Figs 23, 24 Schuchertella? sp. Fig. 23, B 21604, internal mould of pedicle valve, × 2; Fig. 24, B 21569, internal mould of brachial valve, × 2.
 Figs 25-28 Anoplia sp. Fig. 25, BC 6580-1, latex casts of internal moulds of brachial valve (above) and pedicle valve, × 4; Fig. 26a, b, BC 6582, internal mould and latex cast of pedicle valve, × 3; Fig. 27, B 14198, internal mould of brachial valve, × 3; Fig. 28, BC 6583, internal mould of brachial valve, × 4.
- Figs 29, 30 Productella vicaryi (Salter, 1864). Fig. 29a, b, lectotype (here selected), B 21550, internal mould of pedicle valve, figured Salter 1864: pl. 17, figs 16a, b, × 2; Fig. 30, B 21725, internal mould of pedicle valve, figured Davidson 1881: pl. 39, fig. 15, × 2.

but there is no doubt of its generic identification: the Budleigh Salterton species is very like the type species, *Anoplia nucleata* (Hall) and compares very well with specimens (e.g. BC 6629) from the Lower Devonian Camden Chert of Tennessee, U.S.A., except that the American species is relatively narrower and the brachial valve median septum is only rarely and weakly developed in the specimens from Budleigh Salterton.

Suborder **PRODUCTIDINA** Waagen Superfamily **PRODUCTACEA** Gray

Salter (1864) and Davidson (1870) named one productoid species, *vicaryi*, which is reconsidered separately below, but it is probable that there is at least one further productoid present in the Budleigh Salterton pebbles. In particular, a distorted and crushed internal mould of a pedicle valve, B 21723, is not only large (width 37.2 mm, observed length 35.8 mm) but also appears to bear the internal reflection of

external ribbing, unlike *Productella vicaryi* which is not ribbed.

Family **PRODUCTELLIDAE** Schuchert & Le Vene Subfamily **PRODUCTELLINAE** Schuchert & Le Vene

Genus PRODUCTELLA Hall, 1867

Productella vicaryi (Salter, 1864)

- Figs 29-30
- 1864 Leptaena Vicaryi Salter: 296; pl. 17, figs 16, 17.
- 1870 Productus Vicaryi (Salter) Davidson: 87; pl. 6, fig. 14.
- 1881 Productus Vicaryi (Salter); Davidson:351; pl. 39,
 - figs 14, 15.

LECTOTYPE (here selected), B 21550, the internal mould of a pedicle valve, the original of Salter 1864: pl. 17, figs 16a, b; W. Vicary Collection, refigured here as Fig. 29. There is no associated fauna on the pebble fragment. Salter also mentioned two brachial valves, one of which he figured, but their present whereabouts is unknown.

DISCUSSION. There are twelve isolated pedicle valves, four isolated brachial valves and one badly damaged pair of conjoined valves (Ex M 4042, Wyatt-Edgell Collection) and some fragments of external moulds that can be attributed to this species. Some, e.g. B 21725 (Fig. 30), are associated on the same pebbles as Cyrtospirifer verneuilli and an indeterminate unicinuliform (p. 31), and like them vicaryi is thus undoubtedly of late Devonian (Frasnian) age. The species is of variable size, ranging up to Ex M 4042, which is broken, but seen to 34.2 mm in length. Salter's species is attributed here to Productella since it is smooth, the spines are scattered over all of the ventral valve exterior (in contrast to Spinulicosta Nalivkin in which the spines are largely restricted to the flanks and are associated with incipient ribbing), and the muscle fields in both valves are comparable with the type species, P. subaculeata (Murchison) from the Upper Devonian of France. The genus is widespread in Middle and Upper Devonian rocks in Europe, Asia and North America.

Order RHYNCHONELLIDA Kuhn

Rhynchonellides are common in the Devonian pebbles from Budleigh Salterton. However, of all the groups, they present the worst problems of identification since sometimes the preservation is poor, many specimens occur by themselves on single rock fragments, and there is a great deal of both homoeomorphy and also taxonomic division among Devonian rhynchonellides. Three of the species named by Davidson are briefly reviewed below, with illustrations of their type specimens, and the common Frasnian form, identified by Davidson as *Rhynchonella inaurita* Sandberger, is also illustrated. However, three other named forms are not properly reviewed, for various reasons as follows:

(a) '*Rhynchonella elliptica* Schnur?' of Davidson (1870: 81; pl. 5, fig. 4 and 1881: 342; pl. 38, figs 22–25). The illustrations consist of four rhynchonellide specimens, one not traced in the Winwood Collection at Bristol and the others still present in the British Museum (Natural History), Sedgwick Museum and British Geological Survey respectively. The missing Winwood specimen is associated with Upper Devonian spiriferides, but the others are all slightly different in aspect and remain indeterminate here, and of uncertain age.

(b) '*Rhynchonella thebaulti* Rouault' of Davidson (*Rhynchonella* sp. of Davidson 1870: 81; pl. 5, figs 5, 6, and *R. Thebaulti* of Davidson 1881: 342; pl. 38, figs 26–29). Again, three out of the four illustrated specimens survive today, but the ages of all are unknown and Davidson's (1881) figs 26 and 27 may represent a different species from his figs 28 and 29, to judge by the number of ribs on the fold; the specimens remain indeterminate here.

(c) 'Rhynchonella' winwoodiana Davidson (1881: 340; pl. 38, fig. 19). Only a single specimen ever existed and this has not been traced in the Winwood Collection at Bristol City Museum. It was associated on a pebble with two enteletacean pedicle valves which Davidson termed Orthis hamoni Rouault: it is not clear whether this block was of Upper or Lower Devonian age, and, at least until the specimen again comes to light, winwoodiana must remain a nomen dubium.

Superfamily RHYNCHONELLACEA Gray

Genus CAMAROTOECHIA Hall & Clarke, 1893

'Camarotoechia' valpyana (Davidson, 1870) Fig. 33

- 1870 Rhynchonella Valpyana Davidson: 82; pl. 4, figs 26, 27.
- 1881 Rhynchonella Valpyana Davidson; Davidson: 343; pl. 38, figs 33, 34.

LECTOTYPE (here selected), B 20984, the internal mould of conjoined valves, the original of Davidson 1870: pl. 4, fig. 26 and Davidson 1881: pl. 38, fig. 33; R.H. Valpy collection, figured here as Fig. 33.

DISCUSSION. This small rhynchonellid is relatively rare, but, although the lectotype is a detached specimen and therefore intrinsically difficult to date, the species is to be found occasionally on slabs of late Devonian age. Its true generic attribution is uncertain, but it is referred here to 'Camarotoechia' rather than 'Rhynchonella'.

'Camarotoechia' ovalis (Davidson, 1870) Figs 34–35

1870 Rhynchonella? ovalis Davidson: 82; pl. 4, figs 24, 25.
1881 Rhynchonella? ovalis Davidson; Davidson: 344; pl. 38, figs 36, 37.

LECTOTYPE (here selected), B 16359, internal mould of a brachial valve, the original of Davidson 1870: pl. 4, fig. 25 and also Davidson 1881: pl. 38, fig. 37; W. Vicary collection, refigured here as Fig. 34.

DISCUSSION. This species is of Lower Devonian age, and occurs on slabs (e.g. BC 6578) together with *Salopina adventita* sp. nov. (p. 24) and *Leptostrophia etheridgii*. It has approximately 20 ribs and is without a strong fold or sulcus. Its true generic attribution is uncertain, although some features seem similar to *Cydimia* from the Lower Devonian of New South Wales (Chatterton 1973).

Genus KATUNIA Kulkov, 1963

Katunia? vicaryi (Davidson, 1870)

Figs 9, 36–38

- 1870 Rhynchonella Vicaryi Davidson: 82; pl. 7, figs 7, 8.
- 1881 Rhynchonella Vicaryi Davidson; Davidson: 343; pl. 38, figs 30, 31.

LECTOTYPE (here selected), BB 70884, the internal mould of a pedicle valve, the original of Davidson, 1870: pl. 5, fig. 8, also Davidson, 1881: pl. 38, fig. 31; W. Vicary collection, figured here as Fig. 36.

DISCUSSION. This species occurs commonly on the same slabs as *Salopina adventita* sp. nov. (e.g. Fig. 9), and is of Lower Devonian (Lockhovian–Pragian) age. It is referred with some hesitation to *Katunia*, whose type species comes from the Lower Devonian of the Altai Mountains, U.S.S.R.



- Figs 31, 32 Uncinuliform gen. et sp. indet. Fig. 31a, b, BC 6252, internal mould of conjoined valves, figured Davidson 1881: pl 38, figs 35, 35a as *Rhynchonella inaurita*, × 2; Fig. 32, BC 21528, internal mould of pedicle valve, figured Davidson 1870: pl. 5, fig. 3 as *Rhynchonella inaurita*, × 1.5.
- Fig. 33 'Camarotoechia' valpyana (Davidson, 1870). a-d, lectotype (here selected), B 20984, lateral, anterior, ventral and dorsal views of internal mould of conjoined valves, figured Davidson 1870: pl. 14, fig. 26, × 3.
- Figs 34, 35 'Camarotoechia' ovalis (Davidson, 1870). Fig. 34a, b, lectotype (here selected), B 16359, internal mould of brachial valve, figured Davidson 1870: pl. 4, fig. 25, × 3; Fig. 35, BC 6578, internal mould of brachial valve, × 4.
- Figs 36-38 *Katunia? vicaryi* (Davidson, 1870). Fig. 36, lectotype (here selected), BB 70884, internal mould of pedicle valve, figured Davidson 1870: pl. 5, fig. 8, × 2; Fig. 37a-d, B 21530, lateral, ventral, posterior and dorsal views of the internal mould of conjoined valves, × 3; Fig. 38, B 21641, latex cast of external mould of brachial valve, × 3.
- Fig. 39 Athyris? incerta Davidson, 1870. a, b, lectotype (here selected), B 21711, latex cast and internal mould of a brachial valve, figured Davidson 1870: pl. 4, fig. 12, × 2.



Figs 40-42 Nucleospira vicaryi Davidson, 1870. Fig. 40, BC 6584, internal mould of brachial valve, × 1.5; Fig. 41, B 21716, internal mould of pedicle valve, × 1.5; Fig. 42, lectotype (here selected), B 21549, internal mould of brachial valve, figured Davidson 1870: pl. 4, figs 16, 17, × 2.

Indeterminate genus

Uncinuliform species, indet. Figs 31–32

- 1864 Rhynchonella sp. Salter: 296; pl. 17, fig. 15, ?fig. 14.
 1870 Rhynchonella inaurita (Sandberger); Davidson: 80; pl. 5, figs 1–3.
- 1881 *Rhynchonella inaurita* Sandberger?; Davidson: 341; pl. 38, figs 35, 35a, b, ?fig. 21.

This is the most common rhynchonellide in the entire Budleigh Salterton fauna, with more than a hundred specimens in the British Museum (Natural History) and many more in other museums. It is undoubtedly of late Devonian age, since it often occurs on the same pebbles as Cyrtospirifer verneuili. Davidson referred the form to Rhynchonella inaurita Sandberger, apparently with confidence in 1870 but with a query in 1881. I consider the query more than justified, partly because Sandberger & Sandberger's species (1855) is recorded from an enormous range of horizons and localities from within the German Devonian, and partly because the only specimen which they figured (1855: pl. 33, fig. 5) has dental plates, which the Budleigh Salterton species lacks, and also has a much more exaggerated fold and sinus. The form is tentatively identified as an uncinulid here, but is not Uncinulus itself since the ribbing style at the commissure is different.

Order ATRYPIDA Moore Superfamily ATHYRIDACEA M^cCoy Family ATHYRIDAE M^cCoy

Genus ATHYRIS McCoy, 1844

Athyris? incerta Davidson, 1870

Fig. 39

1870 Athyris incerta Davidson: 80; pl. 4, fig. 12.
1881 Athyris incerta Davidson; Davidson: 338; pl. 38, fig. 5.

LECTOTYPE (here selected), B 21711, the original of Davidson, 1870: pl. 4, fig. 12, the internal mould of a brachial valve; W. Vicary collection, refigured here as Fig. 39.

DISCUSSION. Only one pebble containing Athyris? incerta is known, and it contains two well preserved brachial valves (including the lectotype), and one poorly preserved pedicle valve of incerta and a rather poorly preserved enteletacean which, however, can be identified as *Platyorthis monnieri*, thus putting the age of the athyrid as Lower Devonian. The generic attribution is uncertain: the type species of Athyris is *Terebratula concentrica* von Buch, which needs revision but which comes from the mid-Devonian of the Eifel region, Germany. The hinge plates of *incerta* are certainly of athyrid type, but not enough is known of the rest of the morphology to do otherwise than place it into *Athyris*?. Boucot *et al.* (1964: 819) show *Athyris* itself to range from the Siegenian to the Permian, and thus *incerta* would be among the earliest possibly attributable species, but the whole plexus requires both generic and specific re-evaluation.

Family NUCLEOSPIRIDAE Davidson

Genus NUCLEOSPIRA Hall, 1859

Nucleospira vicaryi Davidson, 1870 Figs 40-42, ?Fig. 51

- 1870 Nucleospira Vicaryi Davidson: 79; pl. 4, figs 15-18.
- 1881 Nucleospira Vicaryi Davidson; Davidson: 355; pl. 40, figs 29–31.
- ?1972 Nucleospira sp. Renouf: 122; pl. 26, fig. 10.

LECTOTYPE (here selected), B 21549, the internal mould of a brachial valve, the original of Davidson, 1870: pl. 4, figs 15 (upper right), 16 and 17, and also Davidson, 1881: pl. 40, figs 30 (upper left) and 31; W. Vicary collection, refigured here as Fig. 42.

DISCUSSION. The species is certainly of Lower Devonian age since pebble B 21714 contains both it and also *Salopina adventita* sp. nov. described on p. 24. It has the characteristic median septa in both pedicle and brachial valves and thus Davidson's original generic assignment is still valid.

Order SPIRIFERIDA Waagen Superfamily SPIRIFERACEA Waagen Family DELTHYRIDAE Waagen Subfamily ACROSPIRIFERINAE Termier & Termier

Genus HOWELLELLA Kozlowski, 1929

Howellella cortazari Carls, 1969

Figs 43a, b

- 1870 Spirifera octoplicata Sowerby?; Davidson: 79; pl. 4, fig. 23.
- 1881 Spiriferina octoplicata Sowerby; Davidson: 340; pl. 38, figs 7, 8.
- 1969 Howellella cortazari Carls: 343; pl. 4, figs 21-22.
- 1972 *Howellella* cf. *mercurii* (Gosselet); Renouf: 122; pl. 25, figs 7–9; pl. 26, fig. 1.
- 1985 Howellella cortazari Carls; Gourvennec: 158; pl. 2, figs 10-24.



Fig. 43 Howellella cortazari Carls, 1969. a, b, BB 70944, dorsal and posterior views of internal mould of brachial valve, × 3.
Figs 44-47 Cyrtospirifer verneuili (Murchison, 1840). Fig. 44, B 21542, internal mould of pedicle valve, × 1.5: fig. 45a, b, B 21521, dorsal and posterior views of internal mould of brachial valve, figured Salter 1864: pl. 17, fig. 11 as Spirifer antiquissimus (of which it is the lectotype, here selected), × 1.5; Fig. 46a-c, B 24470, posterior, lateral and dorsal views of brachial valve, × 1.5; Fig. 47, B 21526, internal mould of pedicle valve, figured Davidson 1870: pl. 4, fig. 20 (lower), × 2.

Figs 48-50 *Cyrtospirifer? micropterus* (Davidson, 1870). Fig. 48, BC 6090, internal mould of brachial valve, × 1.5; Fig. 49, B 21527, internal mould of central part of pedicle valve showing muscle field, the original of Davidson 1870: pl. 4, fig. 21, × 1.5; Fig. 50, lectotype (here selected), BB 70886, internal mould of brachial valve, figured Davidson 1870: pl. 4, fig. 22, × 2.

Gourvennec (1985) has revised Lower Devonian Howellella and concluded that the species are best differentiated both by the absolute size and by the numbers of costae. The Budleigh Salterton form never exceeds 13 mm in width (n=10) and has 6–9 costae per flank, indicating in Gourvennec's terms a transition between the large form of *H. mercurii* and *H.* cortazari. Since the type of mercurii is the smaller form (with type specimen from the Lower Gedinnian Mondrepuits Formation of the Ardennes), the Budleigh Salterton species is identified as *H. cortazari*, whose types come from the Lower Gedinnian Nogueras Formation of Aragon, Spain (Carls 1969).

Family CYRTOSPIRIFERIDAE Termier & Termier

Genus CYRTOSPIRIFER Nalivkin, 1919

Cyrtospirifer verneuili (Murchison, 1840) Figs 44–47 1840 *Spirifer Verneuili* Murchison: 252; pl. 2, figs 3a–e.





- Fig. 51 ?Nucleospira vicaryi Davidson, 1870. a, b, BC 6585, dorsal and posterior views of small brachial valve, × 3.
- Fig. 52 Cryptonella? sp. BC 6435, internal mould of brachial valve, × 1.5.
- Fig. 53 Cryptonella? cf. rhenana (Drevermann, 1902). B 21712, internal mould of small brachial valve, × 3.
- Fig. 54 Mutationella? erratica (Davidson, 1870). a-c, Holotype, B 21543, dorsal, lateral and ventral view of internal mould of conjoined valves, \times 3.
- Fig. 55 Mutationella aff. barroisi (Asselberghs, 1930). B 20896, internal mould of brachial valve, × 3.
 - 1864 Spirifer antiquissimus Salter: 295; pl. 17, figs 10-12.
 - 1864 Spirifer Davidis Rouault?; Salter: 296; pl. 17, fig. 13.
 - 1870 Spirifera Verneuilii (Murchison) Davidson: 78; pl. 4, figs 19–20
 - 1881 Spirifera Verneuilii (Murchison); Davidson: 339; pl. 38, figs 9-14.
 - 1882 Spirifera verneuilii (Murchison); Davidson: 35, ?pl. 2, fig. 1.
 - 1942 Spirifer (Cyrtospirifer) Verneuili Murchison; Paeckelmann: 23; pl. 13, figs 2, 3.
 - 1959 Cyrtospirifer verneuili (Murchison) Vandercammen: 114; pl. 4, figs 1–6.

LECTOTYPE of *antiquissimus* (here selected), B 21521, the internal mould of a brachial valve, the original of Salter, 1864: pl. 17, fig. 11; W. Vicary collection, refigured here as Fig. 45.

DISCUSSION. Murchison (1840) described Spirifer verneuili from the Ferques area in northern France from rocks of Upper Frasnian age (Wallace 1969). Davidson (1881, 1882) carefully compared the Budleigh Salterton specimens with the French forms, and came to the conclusion that they were conspecific. When Salter (1864) described Spirifer antiquissimus, he considered that all the Budleigh Salterton fauna was of Ordovician age and thus did not think to compare it directly with the French form from the late Devonian. Cyrtospirifer has been revised in a substantial monograph by Vandercammen (1959), who distinguished fifteen species of the genus and presented many measurements on a substantial number of specimens; however, these were almost entirely from Belgium, and Vandercammen did not revise any topotype specimens of verneuili from Ferques or discuss Murchison's original types except as they were illustrated. Paeckelmann (1942: pl. 3, fig. 2) had figured a young specimen from Ferques, but his systematics in general were discarded by Vandercammen. The whole species group, which occurs in great abundance in the late Devonian of Europe and possibly also elsewhere, is clearly rather complicated and its revision is outside the scope of this paper. Nevertheless, it is worth recording here that there are 11 specimens (registered B 19163-6) all from the 'Boulonnais' area, France (which includes the Ferques inlier), which were collected by Bouchard and were transferred from the Museum of Practical Geology to the British Museum (Natural History) with the rest of its foreign collections in 1905; these probably include at least some of the original specimens used by Murchison in 1840, although Murchison's figures appear rather generalized. Should the Budleigh Salterton form prove distinct from the true Ferques verneuili, then Salter's name antiquissimus would need to be revived.

Cyrtospirifer? micropterus (Davidson, 1870) Figs 48-50

- 1870 Spirifera macroptera Goldfuss? var. microptera Davidson: 79; pl. 4, figs 21, 22.
- 1881 Spirifera speciosa Schlotheim; Davidson: 340; pl. 38, figs 15-18.

LECTOTYPE of *micropterus* (here selected), BB 70886, the internal mould of a brachial valve, the original of Davidson, 1870: pl. 4, fig. 22 (not fig 22a); also figured by Davidson, 1881: pl. 38, fig. 15; W. Vicary collection, refigured here as Fig. 50.

DISCUSSION. Since Davidson's time more than one form of general cyrtospiriferid type has been identified from Budleigh

Salterton pebbles, but Davidson himself changed his mind on the identification. There do appear to be several specimens, including the type specimens of Davidson's variety *microptera*, which are relatively wider than the great bulk of *C. verneuili* specimens described above, and which are provisionally kept distinct here. The ventral interiors also seem different: the *microptera* specimens have a much weaker or even absent median septum, and relatively shorter dental plates; however, these features may be accentuated by the poor preservation (relatively coarse quartzite) of the *microptera* types.

Order TEREBRATULIDA Waagen

Occasional terebratulide specimens are found very rarely in Budleigh Salterton pebbles; Davidson (1870, 1881) illustrated some under the name Terebratula sacculus Martin and another single specimen under the new name of Athyris? erratica. The last specimen, since it was formally named by Davidson, is considered separately below, but the others consist simply of four separate specimens, none of which are worth full description. These are: BC 6435, a large (28.5 mm long) specimen with no ornament, found in the same pebble as late Devonian spiriferids and productids, and uncertainly identified as Cryptonella? sp. (Fig. 52); B 21712, a small (6.9 mm long) specimen (Fig. 53) which Dr A. J. Boucot has suggested may be identified as Cryptonella? cf. rhenana (Drevermann, 1902) of early Devonian age (although there are no internal age criteria from associated specimens); B 20896 (Fig. 55), another small specimen (4.9 mm long), associated with Platyorthis monnieri and therefore of definite early Devonian age, and which is very close to Mutationella barroisi (Asselberghs, 1930) as illustrated by Boucot (1960) from the Gedinnian of the Ardennes; and finally B 1759, not illustrated here, which is merely the external mould of a smooth pair of conjoined valves of general terebratuloid aspect, without associated fauna and thus of uncertain age; it is the original of Davidson, 1881: pl. 38, fig. 1.

Suborder CENTRONELLIDINA Stehli Superfamily STRINGOCEPHALACEA King Family MUTATIONELLIDAE Cloud

Genus MUTATIONELLA Kozlowski, 1929

Mutationella? erratica (Davidson, 1870)

Fig. 54

- 1870 Athyris? erratica Davidson: 80; pl. 4, fig. 13.
- 1881 Terebratula sacculus Martin; Davidson: 337 (pars); pl. 38, fig. 3, ?fig. 2, non fig. 1.
- 1881 Athyris? erratica Davidson; Davidson: 338; pl. 38, fig. 4.
- ?1960 Podolella sp.; Boucot: 320.

HOLOTYPE (by monotypy).⁴ ... The internal cast of one specimen was found by Mr Vicary' (Davidson 1870: 80), B 21543, the original of Davidson, 1870: pl. 4, fig. 13, the conjoined internal mould of both valves; W. Vicary Collection, refigured here as Fig. 54.

DISCUSSION. Davidson (1881: pl. 38, fig. 4a) is inaccurate in showing relatively strong ribs on the figured specimen; the internal mould has only faint ribs near the anterior margin. If the exterior were smooth, then the species would be assigned to *Podolella*; however, the faint ribs make an attribution to *Mutationella* rather more likely. Davidson obviously misinterpreted his own drawings when he later came to write the monograph (1881), since he in fact illustrated the same specimen (B 21543) under both *Terebratula sacculus* (pl. 38, fig. 3) and also *Athyris? erratica* (pl. 38, fig. 4), one drawing with and the other without ribs. The true *sacculus* is a Viséan form (Brunton 1982).

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APPENDIX — REVISED PLATE DESCRIPTIONS FOR DAVIDSON'S MONOGRAPH

In a previous work (1978), I presented revised plate descriptions for Davidson's 'Silurian' Monograph (1886-71) and its supplement (1882-83), which included all of the Lower Palaeozoic (and a very few Upper Palaeozoic) brachiopods dealt with by Thomas Davidson in his grand monograph, apart from those from Budleigh Salterton. These latter were not included partly because they formed a separate part of the Davidson monograph (1881) in which Lower and Upper Palaeozoic forms were mixed and partly because at the time of writing the 1978 work, the Budleigh Salterton species were badly in need of both taxonomic and stratigraphical revision. Since the latter has now been accomplished by Cocks & Lockley (1981) for the Ordovician species and in the present paper for the Devonian species, the opportunity is now taken to give revised plate descriptions for Davidson's 1881 Budleigh Salterton Monograph in a similar style to that of Cocks (1978). Because there is only a single plate (Davidson 1881: pl. 42) of Cornish species, these are also included, largely following the revision of Bassett (1981). Davidson's name for the species (transcribed exactly from his plate descriptions and thus often incorrect by modern standards in the use of brackets, abbreviations etc.) is set in *italic*; the modern identification of the specimens which Davidson drew is shown below in **bold** or **bold italic**. A specimen number has been given where possible: where the specimen has not been traced the symbol 'nt' is used. In each case the Davidson Notebooks have been consulted to check the geological locality and original owner of the specimen, and corrections to the locality or collector or age as printed have been placed in square brackets.

PLATE XXXVIII

Figs

Terebratula sacculus, Martin, sp.

indeterminate terebratulide

1, B 1759; Linford Collection. (Devonian, uncertain age), Budleigh Salterton.

2, 3 Terebratula sacculus, Martin, sp.

4

5

6

9-14

21

Mutationella? erratica (Davidson, 1870) 2, ?B 21543; Vicary Collection. 3, 3a, B 21543; Vicary Collection. (Probable Lower Devonian age), Budleigh Salterton. *Athyris? erratica*, Dav.

Mutationella? erratica (Davidson, 1870) 4, 4a, B 21543; Vicary Collection. (Probable Lower Devonian age), Budleigh Salterton.

Athyris incerta, Dav. Athyris? incerta Davidson, 1870 5, 5a, B 21711 (Davidson errs in stating 'one specimen only' – there are two brachial valves and one pedicle valve on the slab), Vicary Collection. (Lower Devonian), Budleigh Salterton.

Athyris Budleighensis, Dav.

Rhipidomella? budleighensis (Davidson, 1870) 6, B 21512; Vicary Collection. (Upper Devonian), Budleigh Salterton.

7,8 Spiriferina octoplicata, Sow.

Howellella cortazari Carls, 1969 7, BB 70944; Vicary Collection. 8, nt; Winwood Collection. (Lower Devonian), Budleigh Salterton.

Spirifer Verneuilii, Murch. = disjunctus, Phillips

Cyrtospirifer verneuili (Murchison, 1840) 9, BC 6253; T. Davidson Collection ex Vicary. 10, nt, Linford Collection. 11, BC 6254; T. Davidson Collection ex Vicary. 12, GSM 13617; Vicary Collection. 13, B 21526; Vicary Collection. 14, nt, Exeter Museum. All (Upper) Devonian, Budleigh Salterton.

15-18 Spirifera speciosa, Schlothe(i)m

Cyrtospirifer? micropterus (Davidson, 1870) 15, BB 70886; Vicary Collection. 16, B 21527; Vicary Collection. 17, BB 70887; Vicary Collection. 18, B 21574; Vicary Collection. (Upper) Devonian, Budleigh Salterton.

19 Rhynchonella Winwoodiana, Dav.

'Rhynchonella' winwoodiana Davidson, 1870 19, nt; Winwood Collection. (Probably Upper) Devonian, Budleigh Salterton.

20 Orthis Hamoni, Rouault indeterminate enteletacean 20, nt; Winwood collection, same pebble as Fig. 19. (Probably Upper) Devonian, Budleigh Salterton.

Rhynchonella? perhaps Rh. inaurita?

indeterminate rhynchonellide 21, GSM 13905; Winwood Collection. Devonian, Budleigh Salterton.

22-25 Rhynchonella elliptica, Schnur?

indeterminate rhynchonellides

22, nt; Winwood Collection. 23, SM X 1352; Wyatt-Edgell Collection. 24, B 21649; Vicary Collection. 25, GSM 13878; Vicary Collection. (Upper) Devonian, Budleigh Salterton.

26-29 Rhynchonella Thebaulti, Rouault

indeterminate rhynchonellides

26, B 20883; Valpy Collection. 27, nt; Valpy Collection.
28, GSM 13907; Wyatt-Edgell Collection. 29, GSM 13908;
Wyatt-Edgell Collection. (Probably Upper) Devonian,
Budleigh Salterton.

30, 31 Rhynchonella Vicaryi, Dav.

Katunia? vicaryi (Davidson, 1870) 30, BB 70883; Vicary Collection. 31, BB 70884; Vicary Collection. (Lower) Devonian, Budleigh Salterton.

32 Rhynchonella? Dav. indeterminate rhynchonellide 32, nt (notebook clearly states Winwood Collection, rather than Museum of Practical Geology as printed). Devonian, Budleigh Salterton. 33, 34 Rhynchonella Valpyana, Dav.

'Camarotoechia' valpyana (Davidson, 1870)
33, B 20984; Valpy Collection. 34, B 21644; Vicary Collection. (Upper) Devonian, Budleigh Salterton. Rhynchonella inaurita, Sanb.?

- uncinuliform gen. et sp. indet. 35, 35a, BC 6252; Vicary Collection. 35b, B 21528; Vicary Collection. (Upper) Devonian, Budleigh Salterton.
- 36, 37 Rhynchonella ovalis, Dav.
 - *Camarotoechia' ovalis* (Davidson, 1870) 36, 36a, B 20975; Valpy Collection. 37, 37a, B 16359; Vicary Collection. (Lower) Devonian, Budleigh Salterton.

PLATE XXXIX

FIGS

35

- Orthis? hipparionyx? Schuchertella? sp. 1 1, GSM 13509; Wyatt-Edgell Collection. (Lower) Devonian, Budleigh Salterton. Mclearnites rouaulti (Davidson, 1870) Strophomena, sp. 1 1a, 1b (1a is the counterpart of 1b), GSM 13508; Wyatt-Edgell Collection (same slab as Orthis? hipparionyx? above). (Lower) Devonian, Budleigh Salterton. Strophomena? sp. 2 Leptostrophia etheridgii (Davidson, 1870) 2, 2a, GSM 13904. (Lower) Devonian, Budleigh Salterton. 3 Streptorhynchus crenistria, Phillips indeterminate davidsoniacean 3, B 20901; 'Vicary' Collection (should be Valpy). (Probably Lower) Devonian, Budleigh Salterton. 4 Strophomena Budleighensis, Dav. Douvillina? budleighensis (Davidson, 1870) 4, 4a, 4b, B 21538; Vicary Collection. (Upper) Devonian, Budleigh Salterton. 5-7 Strophomena Edgelliana, Dav. Douvillina edgelliana (Davidson, 1870) 5, B 21535; Vicary Collection. 6, 7, 7a, B 21534, lectotype; Vicary Collection. 7b, B 21541; Vicary Collection. (Upper) Devonian, Budleigh Salterton. Strophomena Vicaryi, Dav. 8 Shaleria vicaryi (Davidson, 1870) 8a, 8b, 8c, 8d, B 21537, lectotype; Vicary Collection. (Lower) Devonian, Budleigh Salterton. 9 Strophomena Rouaulti, Dav. Mclearnites rouaulti (Davidson, 1870) 9a, 9b, 9c, B 21540, lectotype; Vicary Collection. (Lower) Devonian, Budleigh Salterton. 10, 11 Strophomena Etheridgii, Dav. Leptostrophia etheridgii (Davidson, 1870) 10, 10a, B 21539, lectotype; Vicary Collection. 11, BC 6087 (on same slab as lectotype); Vicary Collection. (Lower) Devonian, Budleigh Salterton.
- 12, 13 Chonetes, sp.
 12, 13, nt; Davidson Collection ex Wyatt-Edgell. 13a, B 21546; Vicary Collection. (Upper) Devonian, Budleigh Salterton.
- 14, 15 Productus Vicaryi, Salter, sp.

Productella vicaryi (Salter, 1864) 14, B 14007; Davidson Collection *ex* Vicary. 15, B 21725; Vicary Collection. (Upper) Devonian, Budleigh Salterton. 36

1-8 Orthis Monnieri, Rouault.

Platyorthis monnieri (Rouault, 1851) 1a, 1b, 8 (left), B 20940 (the lectotype of *vicaryi*); Valpy Collection. 2, nt; Winwood Collection. 3, nt; Winwood Collection. 4, nt; Winwood Collection. 5, BC 6251; Valpy Collection (the same slab as Fig. 1). 6, nt; Winwood Collection. 7, reconstruction not based on specific specimens. 8 (right), B 13283; Davidson Collection *ex* Vicary. (Lower) Devonian, Budleigh Salterton.

9, 10 Crania transversa, Dav.

Petrocrania transversa (Davidson, 1870) 9, B 16360; Vicary Collection. 10, B 21544, lectotype; Vicary Collection. (Upper) Devonian, Budleigh Salterton.

11-13 Discina Vicaryi, Dav.

Philhedrella? vicaryi (Davidson, 1866) 11, B 21510, lectotype; Vicary Collection. 12, B 21584; Vicary Collection. 13, B 21491; Vicary Collection. (Probable Arenig age), Figs 11 and 12 from Budleigh Salterton, Fig. 13 from a pebble on Chesil Bank, Dorset.

14, 15 Discina incerta, Dav.

Philhedrella? incerta (Davidson, 1870) 14, B 21545, lectotype; Vicary Collection. 15, B 21580; Vicary Collection. (Ordovician or) Devonian, Budleigh Salterton.

16-20 Lingula Lesueuri, Rouault

Ectenoglossa lesueuri (Rouault, 1850) 16, B 21498; Vicary Collection. 17, SM X 1353; Vicary Collection. 18, nt; Winwood Collection. 19, SM X 1354; F.T.S. Houghton Collection. 20, Ex. M: F 2003; 'purchased from a stonebreaker 1870'. (All Arenig), Fig. 19 from the glacial Drift of Ladypool Lane, near Birmingham, the remainder from Budleigh Salterton.

21 Lingula Hawkei, Rouault

24

Lingulobolus hawkei (Ronault, 1850) 21, Ex M: F 6066; T.B. Lear Collection. (Arenig), Woodbury Common [south-east of Exeter, Devon].

22, 23 Dinobolus Brimonti, Rouault, sp.

Lingulobolus brimonti (Rouault, 1850) 22, B 14321; Davidson Collection ex Vicary. 23, GSM 16629; Vicary Collection. (Arenig), Budleigh Salterton. Lingula? Salteri, Dav.

Pseudobolus? salteri (Davidson, 1866) 24, B 14480; Davidson Collection *ex* Vicary. (Arenig), Budleigh Salterton.

25, 26 Lingula Morierei, Tromelin

Lingula' morierei Tromelin, 1876 25, B 21581; Vicary Collection. 26, B 21583; Vicary Collection. (Arenig), Budleigh Salterton.

- 27 Lingula? ?Lingulobolus hawkei (Rouault, 1850)
 27, GSM 16628; Vicary Collection. (Arenig), Budleigh Salterton.
- 28 ? young specimen of *Lingulobolus brimonti* (Rouault, 1850)
 28, B 21578; Vicary Collection. (Arenig), Budleigh Salterton.

29-31 Nucleospira Vicaryi, Dav.

Nucleospira vicaryi Davidson, 1870 29, 30, reconstructed from B 7890 and B 21549; Vicary Collection. 31, B 21549; Vicary Collection. (Lower Devonian), Budleigh Salterton.

PLATE XLI

FIGS

1-9 Orthis Bertho(i)si, var. erratica, Dav.

Corineorthis erratica (Davidson, 1869) 1, nt; Winwood Collection: 2, nt; Winwood Collection. 3, BRSMG Cc 766.1; Winwood Collection. 4, GSM 13472; Vicary Collection. 5, BRSMG Cc 766.2; Winwood Collection. 6, B 20936; Valpy Collection. 7, GSM 13476; Winwood Collection. 8, GSM 5489. 9, GSM 13471, Wyatt-Edgell Collection. (Llandeilo), Budleigh Salterton.

10, 11 Orthis pulvinata, Salter, sp.

Salopia? pulvinata (Salter, 1864) 10, 11, B 21523, lectotype; Vicary Collection. (Llandeilo), Budleigh Salterton.

12-20 Orthis Budleighensis, Dav.

Tafilaltia valpyana (Davidson, 1869) 12, B 21616, including (centre left) the lectotype of *bud-leighensis*; Vicary Collection. 13, nt; Winwood Collection. 14, nt; Winwood Collection. 15, reconstructed from B 21611 and B 21626; Vicary Collection. 16, GSM 13480; Vicary Collection. 17, GSM 13496; Wyatt-Edgell Collection. 18, ?GSM 13483; Wyatt-Edgell Collection. 19, GSM 13496a; Winwood Collection. 20, nt in Cambridge. (Llandeilo), Budleigh Salterton.

21, 22 Orthis Valpyana, Dav.

Tafilaltia valpyana (Davidson, 1869) 21, reconstructed from B 21533 and B 21524; Vicary Collection. 22, B 21533; Vicary Collection. (Llandeilo), Budleigh Salterton.

23 Terebratula? sp.

monoplacophoran, perhaps Vallatotheca sp. 23, B 21531; Vicary Collection. (Llandeilo), Budleigh Salterton.

PLATE XLII

Figs

1-6 Strophomena grandis, Sow.

Corineorthis cornubiensis (Davidson, 1881) 1, RGSC 633; Peach Collection. 2, nt RGSC but Davidson cast within B 13657; Peach Collection. 3, nt RGSC, but Davidson cast within B 13657; Peach Collection. 4, composite reconstruction from Peach Collection specimens. 5, nt RGSC but Davidson cast within B 13657; Peach Collection. 6, nt RGSC; Peach Collection. (Llandeilo), Carn (Rocks), Gorran (Haven), Cornwall.

7-10 Orthis calligramma, var.

Schalidomorthis stubblefieldi Bassett, 1981 7, RGSC 1044; Peach Collection. 8, 9, GSM 10378; Peach Collection. 10, nt RGSC but Davidson cast B 13065; Peach Collection. (Llandeilo), Carn (Rocks), Gorran (Haven), Cornwall.

11, 12 Orthis scotica? McCoy, sp.

Schalidomorthis stubblefieldi Bassett, 1981 11, RGSC 661; Peach Collection. 12, nt Truro Museum. (Llandeilo), Gorran Haven, Cornwall.

Orthis sp.? indeterminate orthide
 13, nt RSM but Davidson cast B 13306; Peach Collection.
 (Llandeilo), Carn (Rocks), Gorran Haven, Cornwall.

14, 15 Orthis Berthoisi, var. cornubiensis, Tromelin.

Corineorthis cornubiensis (Davidson, 1881) 14, 15, BB 73794, lectotype, ex Truro Museum; Peach Collection. (Llandeilo), Caerhayes, Cornwall.

16-25 Orthis Budleighensis.

- 16, 18, 19, RSM 1951.5; Peach Collection. 17, nt RGSC;
 Peach Collection. 20, nt RGSC; Peach Collection. 21, nt RGSC; Peach Collection. 22, RGSC 943; Peach Collection. 23, GSM 10374; Wyatt-Edgell Collection. 24, nt GSM;
 Etheridge Collection. 25, GSM 10334; Wyatt-Edgell Collection. (Llandeilo), Figs 16–19 from Carn rocks, Gorran Haven, Figs 21, 22 from Gerrans Bay, and Figs 20 and 23–25 only labelled Gorran Haven, Cornwall.
- 26

Orthis testudinaria, Dalman type.

Dalmanella testudinaria (Dalman, 1828) 26, Naturhistoriska Riksmuseet, Stockholm, one of a type lot of over 70 specimens; Dalman Collection. (Ashgill), Borenshult, Ostergötland, Sweden.

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